The effect of pulsing on macrophyte productivity and nutrient uptake: A mesocosm experiment

Christopher J. Anderson and William J. Mitsch

School of Natural Resources, The Ohio State University

Introduction

Wetland plant productivity and nutrient uptake can be influenced by hydrological parameters including flood depth (Waters and Shay, 1992; Newman et al. 1998; Kellogg et al., 2003), duration (Newman et al., 1998) and flooding frequency (Giovannini and Da Motta Marques, 1998; Tanner, 1999; Casanova and Brock, 2000). Further, water level fluctuations associated with a pulsing hydrology may increase wetland productivity and nutrient uptake (Mitsch and Ewel, 1979; Mitsch et al., 1979; Junk et al., 1989; Odum et al., 1995; Day et al., 2000). Pulsing water regimes are often indicative of riparian wetlands adjacent to flashy streams or rivers in the Midwest United States (Baker et al., 2004). Inflowing flood pulses usually occur sporadically throughout the year and can be laden with higher than normal concentrations of nutrients that can provide a "fertilizing effect" for plant growth (Spink et al., 1998). Further increases in nutrient availability can occur in wetland sediments by the release of phosphorus during anaerobic conditions. However, prolonged wetland inundation increases the potential for anoxic conditions that can be detrimental to macrophyte vegetation (van der Valk and Davis, 1978). The temporary nature of river flood pulses often leads to rapidly dropping water levels, thus decreasing the chance for soil anoxia while increasing nutrient mineralization and the potential for greater macrophyte productivity (Mitsch and Rust, 1984). The benefit of a pulsing hydrology has been well demonstrated for wetland forests (Mitsch et al., 1991; Brown, 1981) and planktonic communities (Hein et al., 1999), but has been less predictable for herbaceous

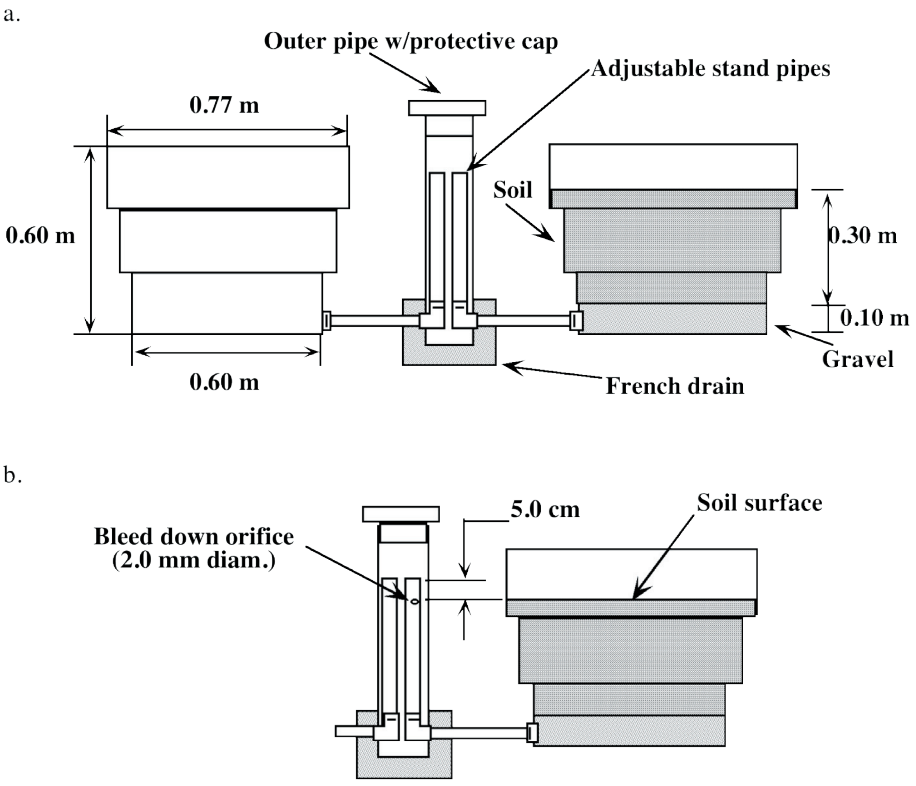

Figure 1. Experimental wetland mesocosms used in this study. Cross-section view and dimensions of two mesocosms and associated French drain system. Water depth was controlled by the height of the connected 'J'-tube extending from the mesocosm tub. Bleed-down orifices were installed at the soil elevation of each mesocosm soil elevation.

wetlands. Herbaceous wetland vegetation may be more sensitive to the variable conditions (depth, duration, etc.) associated with flooding waters that may make a pulsing effect more difficult to detect.

The purpose of this study was to determine if a pulsing hydrologic regime would elicit morphological and functional responses by two wetland plants in experimental wetlands. This project was conducted in conjunction with the first year of a multi-year experiment using two full-scale created wetlands to examine the effects of a pulsing regime. We hypothesized that productivity and nutrient uptake would be affected by water regime, and that pulsing river water into wetlands would result in more efficient N uptake and enhanced primary productivity compared to a steady flow regime.

Methods

The project was conducted at the 12-ha Olentangy River Wetland Research Park at The Ohio State University in Columbus, Ohio, USA (approximately 83.039°W longitude and 40.033°N latitude). A total of twenty mesocosm tubs (Fig.1; area = 0.9 m^2, volume = 540 liters) were used. In each mesocosm a total of 8-10 cm of pea-size gravel was placed in the bottom to allow collection of seepage. Approximately 30 cm of on-site alluvial, upland soil (Ross and Eldean series, consisting of silt loam, silt clays and clay loams; Mcloda and Parkinson, 1980) was placed on top of the gravel. Water levels were controlled with a French drain system established for each mesocosm using 5 cm diameter pvc pipes (Fig. 1). The control structure (top of the pipe) was established 5 cm above the soil layer. To provide gradual water subsidence, a bleed down orifice (2 mm hole) was drilled into the side of each control pipe at the mesocosm soil elevation.

To evaluate the effect of pulsing, mesocosms were randomly assigned to one of four treatments based on macrophyte species and hydrology (Table 1). In March 2002, a total of 30 rhizomes each of *Typha angustifolia* L. (narrow-leaved cattail, hereafter *Typha*) and *S. tabernaemontani* (C.C. Gmelinm) Palla (soft-stemmed bulrush, fka *Scirpus validus*, hereafter *Schoenoplectus*) from a Midwestern nursery were trimmed to approximately 25 ± 5 g in size and planted 3 cm below the soil surface. Three rhizomes (with no inter-species mixing) were planted in each mesocosm. To expedite growth of the planted rhizomes, wetlands were kept in moist condition throughout summer and autumn 2002 with groundwater equally distributed to all the mesocosms. At the end of August 2002, initial condition aboveground biomass was non-destructively estimated in each mesocosm by relating various morphological parameters to reference plants. For Schoeneplectus, stem density, mean stem height, number of flowers, and mean maximum stem height were recorded. For Typha, the number of leaves per ramet, ramet density, mean ramet height, number of flowers, and mean maximum ramet height were recorded. Over the winter of 2002-2003, the mesocosms were not watered; a layer of snow and ice covered them throughout most of the season.

In March 2003 it was discovered that Muskrats (*Ondatra zibethicus*) excavated 3 *Schoenoplectus* wetlands of nearly all its rhizomes during winter 2002-03. In April 2003, *Schoenoplectus* was sodded from control wetlands used in another mesocosm experiment, and transplanted into the disturbed mesocosms. Each disturbed mesocosm received five pieces of *Schoenoplectus* sod that were approximately 15 x 20 cm wide and 4 cm thick. All measurements from these mesocosms were analyzed separately and designated as 'Schoenoplectus (1-yr)' wetlands, compared to '*Schoenoplectus* (2-yr)' for the undisturbed wetlands (Table 1).

During the experimental 'wet season' (April through June 2003), water was pumped from the Olentangy River based on the pulsing regiment in Table 1. By design, all mesocosms received a near equivalent monthly hydrologic load of 160 cm month-1.

Water was pumped directly from the Olentangy River to the mesocosms via a low-pressure pump and an elevated reservoir tank system. A garden hose was used for each water regime and extended to each mesocosm. At each nexus point, the hose was attached to the mesocosm rim and a volume-adjustable irrigation sprayer (Raindrip® R180C) was used to control the amount of water pumped into each mesocosm. In mid-May 2003, the pumping schedule was postponed for 11 days to repair the pumping system.

Pumping volumes and water depths were recorded for each water regime. Three mesocosms were omitted from the study in 2003 because of faulty drainage systems that developed and could not be repaired. During the experimental wet season, a 250 mL sample of the pumped river water was collected weekly and analyzed for NO_3-NO_2 and total P using a Lachat QuikChem IV automated system and Lachat methods (U.S. EPA, 1983). Total P was analyzed using the ascorbic acid and molybdate color reagent methods after digesting with 0.5 ml of 5.6N H_2SO_4 and 0.2 g NH_3SO_4 to 25ml of sample and exposing the samples to a heated and pressurized environment for 30 minutes in an autoclave. Using the Lachat automated system, nitrate-nitrite was analyzed using the cadmium reduction method. Nutrient concentrations were used with pumping rates to estimate weekly NO_3-NO_2 and total P nutrient loads into the mesocosms.

Plant morphology was measured on 18 June, 23 July and 28 August 2003 using the same parameters measured in September 2002. After the August 2003 measurements, all aboveground vegetation in each mesocosm was harvested and the mesocoms were covered until below ground biomass was harvested. Harvested aboveground material was air-dried and a subsample was oven dried for 3 d (or until constant mass was achieved) at 80° C. Total aboveground biomass was calculated and converted to g m^{-2} for comparison.

In September 2003, soil from each mesocosm was extracted and carefully washed from all root material. A subsample of root material was air dried for 5 d at 105° C

or until constant mass was achieved. Total belowground biomass was estimated for each mesocosm and converted to g m^{-2} for comparison. Below ground biomass data was combined with above ground data in August 2003 to calculate total biomass and the mean root:shoot ratio.

To estimate tissue nutrient concentrations for each mesocosm, 10 mature leaf-stems were randomly selected and analyzed for nutrient content. Tissue specimens were air dried, grounded to pass through a 2 mm sieve and mixed to make a homogenous sample. In mesocosms where significant plant senescence occurred, 10 random senescent stems were analyzed separately from the living stems. All tissue specimens were sent to Service Testing and Research (STAR) Laboratory, Ohio Agricultural Research and Development Center, Wooster, Ohio and analyzed for total N and P. Samples were digested with $HClO_4/HNO_3$ and analyzed for total P by inductively coupled plasma emission spectrometry (Isaac and Johnson, 1985). Samples were analyzed for total N through combustion analysis (AOAC, 1989). Using mean nutrient concentrations, the mean N:P ratio of the aboveground tissue was calculated for all treatment types and compared to thresholds developed by Koerselman and Meuleman (1996) to detect possible community level N or P limitations. As an overall index for site fertility, tissue nutrient concentrations were used with peak biomass measurements in August 2003 to calculate total nutrient uptake for each wetland.

Statistical Analyses.

For each species group [*Typha*, *Schoenoplectus* (1-yr) and *Schoenoplectus* (2-yr)], independent t-tests were used to compare the means of macrophyte parameters (morphological measurements, productivity and nutrient uptake) and mean nutrient loads (mg total P and NO_3-N wk^{-1}) between the pulsed and steady-flow mesocosms. In the case of root:shoot ratios and leaf-tissue N and P concentrations, *Schoenoplectus* (1-yr) and (2-yr) data were comparable ($P<0.05$, t-test) and therefore pooled. A two-way analysis of variance (ANOVA) was conducted to compare the factors of hydrology (pulsed and steady flow wetlands), vegetation, and hydrology-vegetation. For all comparative tests, mean P-values <0.05 were considered significant and P-values <0.01 were considered highly significant. Tests for variance, normality and t-tests were conducted using Minitab Release 14 (Minitab, Inc., 2003), and two-way ANOVAs were conducted using Systat v.10.2 (Systat Software Inc., 2002).

Results

Hydrology and Water Depths

River water was pumped into the wetland mesocosms between 3 April and 18 August 2003. Three week-long pulses of river water occurred during the experimental wet season (between 3 April and 21 July 2003, Fig. 2) to simulate spring and early summer flood pulses typical of the region. From 22 July and 18 August 2003, all mesocosms received an equivalent load (approximately 32 cm wk^{-1}) (Fig. 2). In the pulsed wetlands, weekly mean water depths were 6.7 ±2.4 cm during the non-pulsing weeks and rose to

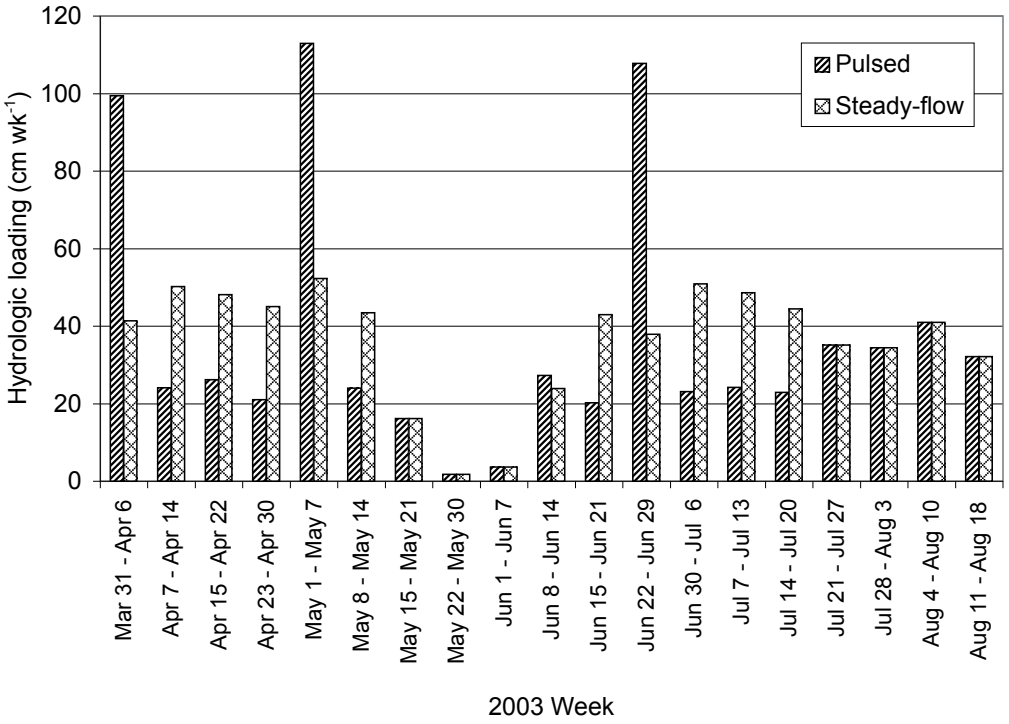

Figure 2.Weekly hydrologic loading rate of pulsed and steady flow mesocosms. Total loading input includes pumped river water and rainfall. Pulsed and steady-flow mesocsosms received 698 and 694 cm, respectively during the 2003 experimental period. Pulsing occurred on the weeks of 31 March, 1 May and 22 June

15.3 ±0.8 cm during the three pulsing weeks. The steady flow wetlands maintained a more consistent mean water level of 11.2 ±1.1 cm. Based on the measurements taken during the experimental wet season, water levels were at or below the surface (<1 cm) 16.4% of the time for pulsed wetlands and 6.9% of the time for steady-flow wetlands. Water levels fluctuated weekly and monthly based on the prescribed loading rates and other environmental factors including rainfall, evapotranspiration, and apparent differences in permeability. Mean water depths of all mesocosms progressively decreased throughout the growing season as temperatures increased and as evapotranspiration increased.

Plant Morphology and Primary Productivity

There was no significant difference in peak dry-weight biomass between the pulsed and steady-flow mesocosms for *Typha* or *Schoenoplectus* (1-yr and 2-yr) (Fig. 3). The highest mean above-ground biomass was recorded in the steady-flow Typha wetlands (1032 ±53 g m^{-2}) while pulsed Schoenoplectus (1-yr) wetlands had the lowest (296 ±58 g m^{-2}). Pulsed Typha wetlands had the highest below ground biomass (1551 ±160 g m^{-2}) and the highest overall (above and below ground) biomass (2557 g m^{-2}) while pulsed Schoenoplectus (1-yr) wetlands had the lowest overall biomass (800 g m^{-2}).

By early August, all Schoenoplectus wetlands had some senesce of mature culms, particularly in the 2-yr, steady-flow wetlands (Fig. 3). By the end of August, the mean dry weight of senescent biomass in the 2-yr, steady-flow wetlands was 234 ±89 g m^{-2}, or approximately 38% of the live biomass dry weight. A comparable distribution (32%) occurred in the pulsed Schoenoplectus (2-yr) wetlands. The Schoenoplectus (1-yr) wetlands had lower percentages of senescent biomass for both steady and pulsed wetlands (14% of the live dry weight for both wetland types). Between July and August new Schoenoplectus shoots emerged; however a substantial amount of the aboveground stems had yellowed by the end of August 2003.

The mean root:shoot ratios for all vegetation groups ranged between 1.4 (steady-flow *Typha* wetlands) and 1.7 (steady-flow *Schoenoplectus* [1 yr] wetlands) in August 2003. No differences in root:shoot ratios were detected when the factors hydrology ($F_{1,13}=0.021$, $P=0.89$), vegetation ($F_{1,13}=0.934$, $P=0.35$) or hydrology-vegetation ($F_{1,13}=0.800$, $P=0.39$) were analyzed.

Plant morphology measurements were generally similar between pulsed and steady-flow wetlands for all three vegetation groups. Mean *Typha* ramet density was highest for pulsed wetlands in August 2003 with 97 ±4 ramets m^{-2}; however both pulsed and steady-flow wetlands averaged over 95 ramets m^{-2} by mid-July (Fig. 4). Pulsed and steady-flow *Typha* wetlands also had similar monthly trajectories in mean ramet height (Fig. 4), mean number of flowers, mean

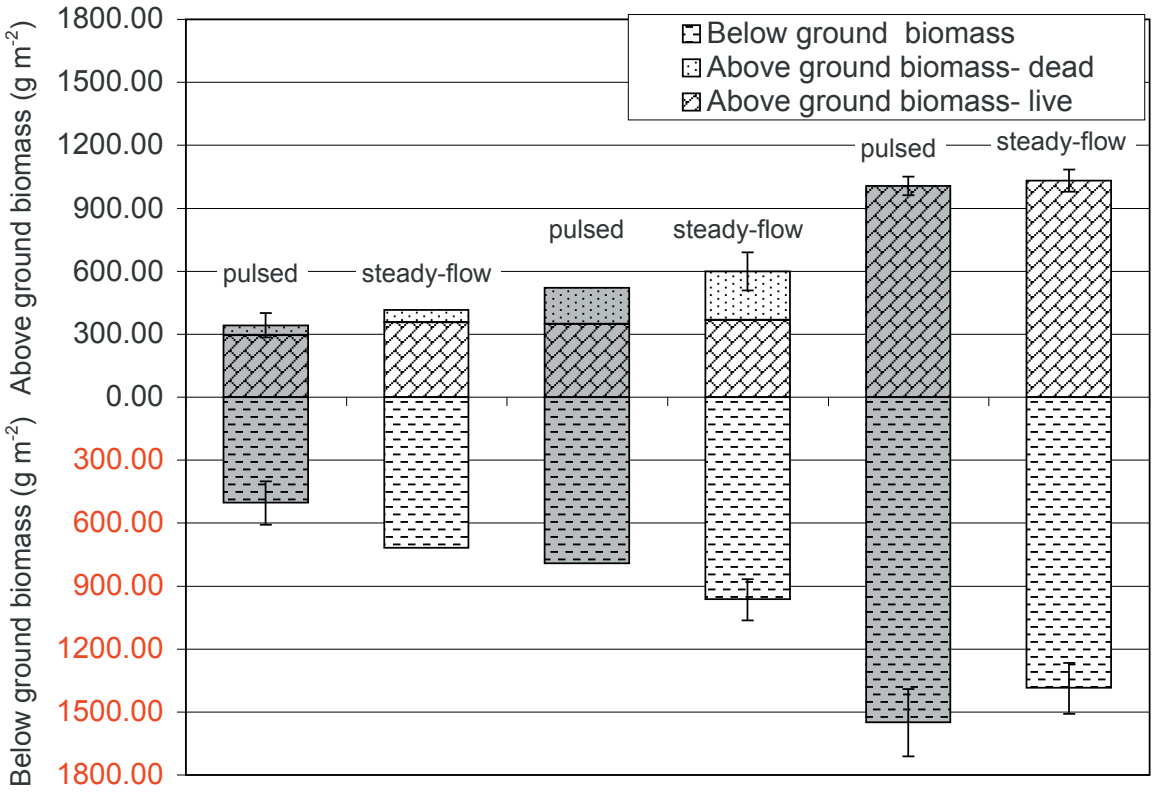

Figure 3. Mean (+ 1 std. error) aboveground and belowground biomass (g m^{-2}) for Schoenoplectus (1^{-yr}), Schoenoplectus (2-yr) and Typha mesocosms at August 2003. Above ground standard error represents total (live and dead) biomass

number of leaves/ramet, and mean maximum ramet heights. *Schoenoplectus* (1-yr and 2-yr) wetlands were more variable than *Typha* between pulsed and steady-flow wetlands but no significant differences were detected (Fig. 4). Senescence of mature stems between July and August reduced mean stem density and stem height of all Schoenolectus wetlands, except steady-flow *Schoenoplectus* (1-yr) which had a density of 452 stems m^{-2} in August. Despite the higher percentage of senescence, *Schoenoplectus* (2-yr) wetlands still had greater mean stem length than the *Schoenoplectus* (1-yr) wetlands.

Plant tissue nutrient concentration

Nutrient levels were comparable between *Schoenoplectus* (1-yr) and (2-yr), and therefore were combined to analyze hydrological regime effects on plant tissue nutrient concentrations. Analysis of plant tissue indicated that there were no significant differences in N or P concentrations for pulsed and steady-flow *Typha* or *Schoenoplectus* wetlands (Table 2). However, when N:P ratios were analyzed, a significant difference was detected for hydrology (pulsed and steady-flow wetlands) ($F_{1,13}$=9.95, P<0.01) (Table 2). No differences in N:P ratios were detected when vegetation ($F_{1,13}$=0.021, P=0.89) or hydrology-vegetation ($F_{1,13}$=0.463, P=0.51) were analyzed. For all mesocosms combined, the mean N:P ratios were 9.2 ±0.6 for steady flow wetlands and 11.7 ±0.5 for pulsed wetlands. For senescent *Schoenoplectus* tissue, no difference was detected in N and P concentrations between steady-flow (11.0 ±0.5 mg N g^{-1} and 0.9 ±0.1 mg P g^{-1}) and pulsed (12.2 ±0.9 mg N g^{-1} and 1.0 ±0.0 mg P g^{-1}) wetlands. Using the N:P ratios calculated for each hydrology and species type, a comparison was made to threshold values determined by Koerselman and Meuleman (1996) (Fig. 5). In all cases, the N:P ratios were less than the 14:1 ratio which indicates that the wetlands were nitrogen limited.

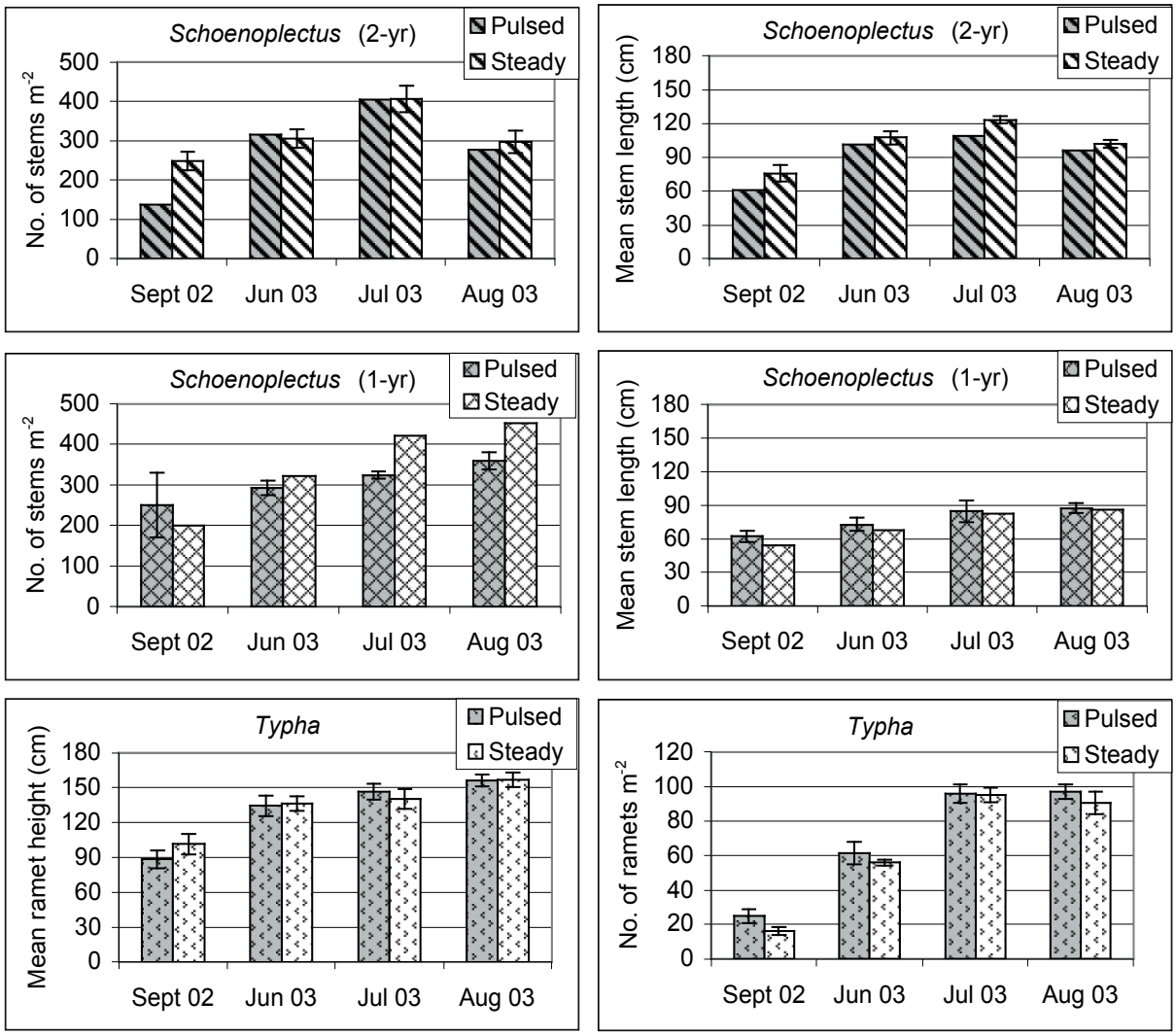

Figure 4.Mean stem length/ramet height (cm) and density of Schoenoplectus (1-yr) and (2-yr) and Typha for pulsed and steady-flow wetlands in September 2002, June 2003, July 2003 and August 2003.

Table 1. The species and experimental hydrology for experimental wetland mesocosms in 2002 and 2003. The use of 'Schoenoplectus (1-yr)' mesocosms was necessary due to muskrat damage during winter 2002.

No. of mesocosms	Species Planted	No. of growing seasons	Hydrology- Monthly Pumping Regiment during Experimental Wet Season
1	*Schoenoplectus*	2	Pulsed - 100 cm/week during week 1, 20 cm/week during weeks 2, 3 and 4
4	*Schoenoplectus*	2	Steady flow - 40 cm/week during all weeks
2	*Schoenoplectus*	1	Pulsed - 100 cm/week during week 1, 20 cm/week during weeks 2, 3 and 4
1	*Schoenoplectus*	1	Steady flow - 40 cm/week during all weeks
5	*Typha*	2	Pulsed - 100 cm/week during week 1, 20 cm/week during weeks 2, 3 and 4
4	*Typha*	2	Steady flow - 40 cm/week during all weeks

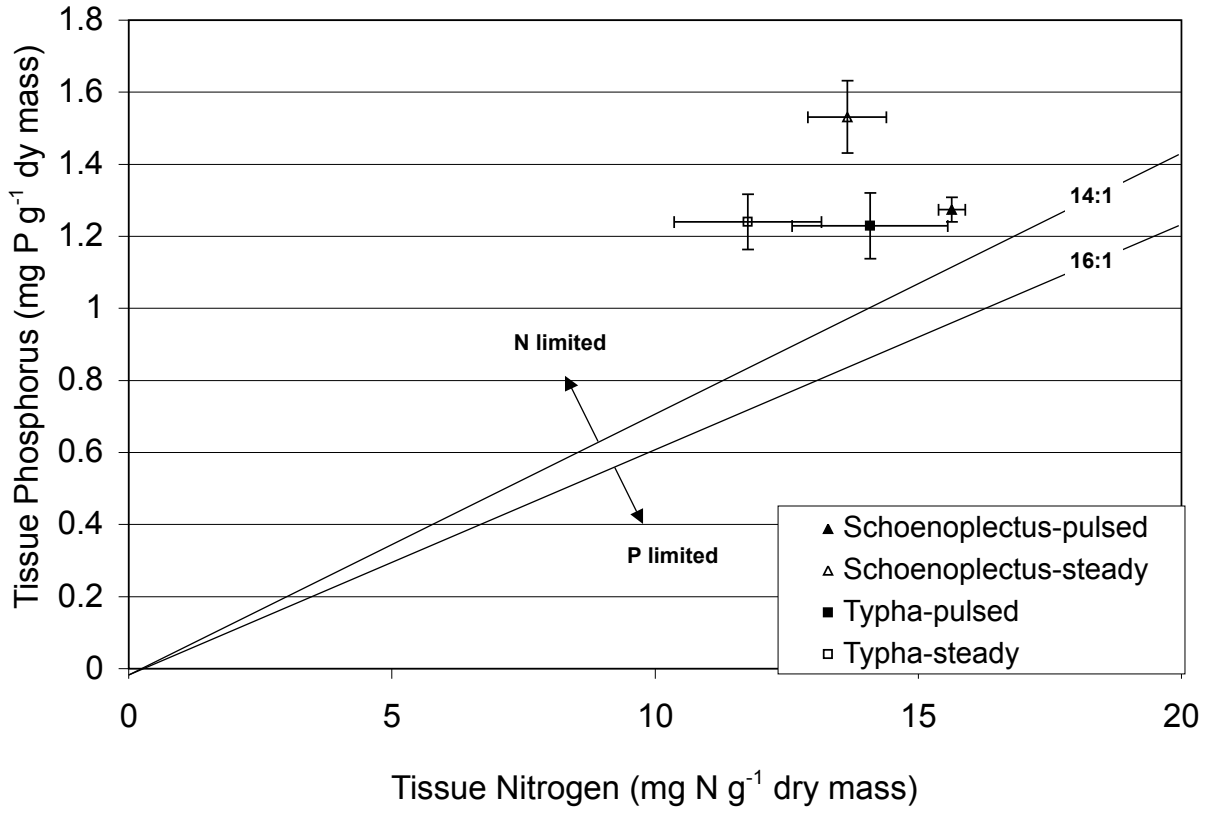

Figure 5. Mean N and P concentrations (+1 SE) of plant tissue of wetland mesocosms in August 2003. Ratios of <14:1 and >16:1 are indications of N and P limitations, respectively (Koerselman and Meuleman, 1996).

Nutrient Loading and Uptake

A weekly mean nutrient loading rate was estimated for pulsed and steady flow wetlands using the weekly hydrologic loading rates and river water nutrient concentrations. The mean nutrient loading rates to each mesocosm were similar: 1372 ±317 mg NO_3-N wk^{-1} and 49 ±17 mg total P wk^{-1} for pulsed wetlands and 1289 ±170 mg NO_3-NO_2 wk^{-1} and 52 ±13 mg P wk^{-1} for steady flow wetlands.

Using the N and P tissue concentrations and plant biomass in August 2003 to compare treatments, pulsed *Typha* wetlands accumulated the most nitrogen (14.4 ±2.0 g N m-2) while steady-flow *Typha* wetlands accumulated the most phosphorus (1.3 ±0.1 g P m^{-2}). No significant differences were detected among hydrological regimes for any of the vegetation groups (Fig. 6).

Discussion

Plant Morphology and Primary Productivity

The pulsing hydrology did not have a substantial effect on *Typha* or *Schoenoplectus* primary productivity when compared to the steady-flow wetlands in this mesocosm study. In terms of overall productivity, *Typha* was more productive than *Schoenoplectus*. *Typha* had exceptional growth during the first two months of the 2003 growing season, accumulating over 60% of its 2003 above ground peak biomass by mid-June. These observations are consistent with other studies that have evaluated *Typha* and shown that it can be highly productive early in the growing season (Martin and Fernandez, 1992; Garver et al., 1988). The range of *Typha* above-ground dry weight biomass was

Table 2. Summary of two-way ANOVA examining the responses of tissue nutrient content and N:P to vegetation type (Typha or Schoenoplectus) and hydrology (pulsed or steady-flow) for wetland mesocosms in 2003.

		Tissue N (mg N g-1)			Tissue P (mg P g-1)			N:P		
Source	df	MS	*F*	*P*	MS	*F*	*P*	MS	*F*	*P*
Vegetation	1	3.942	0.597	0.45	0.059	1.609	0.23	0.055	0.021	0.89
Hydrology	1	8.161	1.236	0.29	0.137	3.748	0.08	25.626	9.945	<0.01
Vegetation x Hydrology	1	3.318	0.502	0.49	0.123	3.351	0.09	1.192	0.463	0.51
Error	13				0.037			2.577		

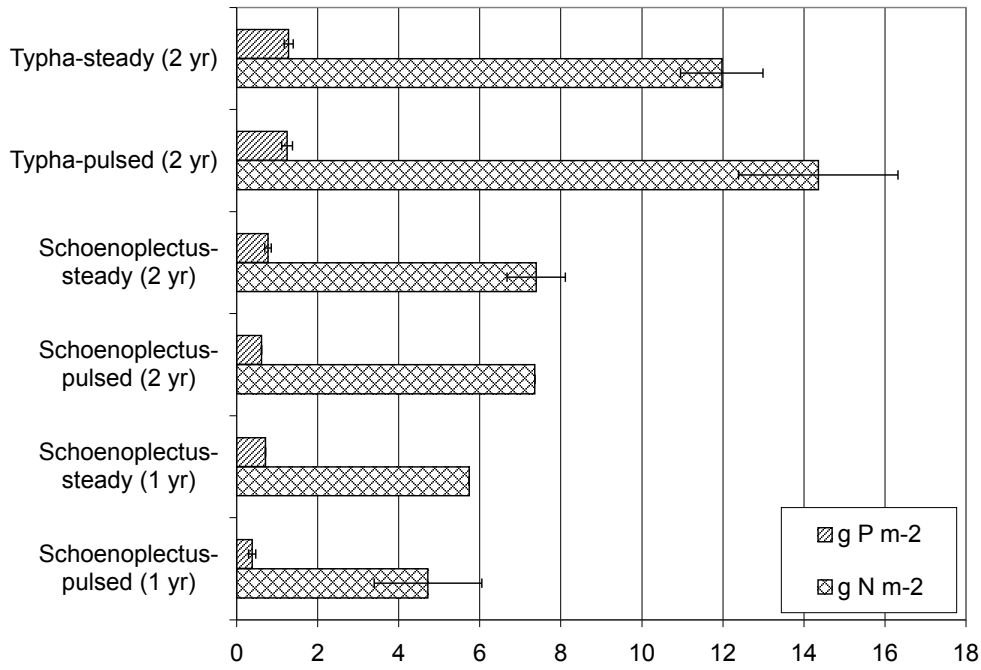

Figure 6. Mean N and P uptake (+1 SE) in wetland mesocoms based on plant tissue concentration and peak biomass (measured in August 2003). Schoenoplectus nutrient uptake is based on live and dead biomass

consistent with other wetland studies (Dubbe et al., 1988; Mason and Bryant, 1975). The root:shoot ratios calculated in this study were within the range (0.9-1.2) found by Kvet and Husak (1978) for *T. angustifolia* in pond littoral zones in Czechoslavakia. However, Farnsworth and Meyerson (2003) found that *T. angustifolia* in Connecticut tidal marshes had lower above ground biomass (800+ g m^{-2}) but greater root:shoot biomass (2.5 ±0.1).

Schoenoplectus productivity was low compared to literature ranges for natural wetlands but comparable to other mesocosm studies. In a literature review conducted by Tanner (2001), peak biomass of *S. tabernaemontani* ranged widely between 400-1400 g m^{-2} for natural marshes in North America. However, in mesocosm studies, the ranges found in this study are more typical. Ahn and Mitsch (2002) evaluated *S. tabernaemontani* productivity in a two-year mesocosm study, maintaining water levels at 10 cm depth and a hydrologic loading rate of 51.1 cm wk^{-1} and 37.1 cm wk^{-1} during the two years, respectively. The mean net annual primary productivity of above ground *Schoenoplectu*s biomass was 425 ±33 g m^{-2} (prior to an imposed correction factor). In another two-year mesocosm study conducted by Svengsouk and Mitsch (2001), mean above ground Schoenoplectus biomass was greater than 350 g m^{-2} for control wetlands and between 450 and 600 g m^{-2} for wetlands fertilized with N, P and both. For their study, groundwater was used and depth was maintained at the soil surface.

The early senescence by *Schoenoplectus* by mid-August was unexpected. In their review of seed bank and vegetation dynamics in prairie pothole wetlands, van der Valk and Davis (1978) reported that the rhizomes of Schoenoplectus do not tolerate prolonged high water levels and anoxic/anaerobic conditions. They partially contributed this condition and the resulting decline *Schoenoplectus* to the degenerating vegetation phase of the prairie pothole marsh cycle (van der Valk and Davis, 1978). In our study, there was evidence (e.g., the flocculation of iron along the outflow stand pipes) that soils were highly reduced and iron was being released. However, this condition may have been partially caused by the sunken position of the mesocosm wetlands. It has been demonstrated that mesocosm wetlands can be susceptible to stagnation because of their small size and sunken position make them less exposed to wind fetch (Ahn and Mitsch, 2002).

While the prescribed water regimes produced a discernable difference in hydrology between the pulsed and steady-flow wetlands, the conditions in this experiment may have been more influenced by the high monthly hydrologic loading rate for all the wetlands. The loading rates were designed to be comparable to the experimental rates prescribed for the full-sized ORW wetlands and were adjusted slightly to accommodate the holding capacity of the mesocosm tubs. The monthly hydrological loading rate used in this study was considerably high when compared to other managed wetlands and with a greater difference between hydrology treatments (e.g., if no pumping had occurred between the pulsing weeks) we may have seen greater morphological differences among the treatment groups.

Plant Tissue Nutrient Concentrations and Uptake

No significant differences between the hydrological regimes were detected for N and P concentrations separately, but based on N:P ratios, steady-flow wetlands were more N-limited than their pulsed counterparts. It is possible that hydrology affected the availability of both N and P. Steady-flow wetlands remained inundated longer and had the potential to lose more N through denitrification than pulsed wetlands, but based on the tissue nutrient data, it appears that P was the more responsive nutrient to hydrology. The longer periods of anoxic/anaerobic conditions in the steady-flow wetlands may have released more P from the sediment. Evidence of highly reduced conditions, including the flocculation of Fe on the stand pipes, suggests that P (associated with Fe) may have been released during the experimental period, enhancing biomass production. Bayley et al. (1985) found that merely the presence of standing water, regardless of its nutrient content, can influence marsh primary productivity and credited this to the release of P that is triggered by the onset of anoxic conditions. It is possible that the vegetation in steady-flow wetlands had some added uptake of P relative to N which would explain their slightly lower N:P ratio compared to pulsed wetlands. While the difference between N:P ratios may or may not be biologically significant, the statistical difference is noteworthy considering the high hydrologic loading rate and the high N load in the river water during much of the experimental period. Inflowing river water was high in NO_3-N relative to P (approximately 26:1), but still resulted in plant tissue N:P ratios below 14:1.

When N:P ratios were examined using the thresholds developed by Koerselman and Meuleman, (1996) vegetation was considered N limited in both water regimes. These values are consistent with the results of other N:P ratios from North American marsh studies cited from the literature by Bedford et al. (1999), although their mean N:P ratio was less (7.5 ±0.7) than either the mean pulsed (11.7 ±0.5) or steady-flow (9.2 ±0.6) ratios calculated in this study. The individual ranges of N and P concentrations and uptake observed in this study are consistent with similar studies. Cronk and Fennessy (2001) reported *Typha* spp. leaf tissue can range from 5-32 mg N g^{-1} and 1-5 mg P g^{-1}. Mason and Bryant (1975) found *T. angustifolia* N:P ratio was 9.5:1 at peak biomass in the Broadland region of Norfolk, England. For *Schoenoplectus*, it is likely that significant translocation of nutrients occurred to below ground tissue prior at the onset of senescence and that N and P levels were even higher in July when most *Schoenoplectus* wetlands were at peak biomass. Tanner (1996) reported that for second-year *Schoenoplectus* growth treated with wastewater effluent, N levels were between 9.2 and 12.9 mg g^{-1} and P levels between 2.2 and 3.5mg g^{-1}. These nitrogen levels are comparable to those found in this study with the phosphorus

levels slightly higher.

Implications for the Full-sized Wetland Pulsing Study

Pulsing effects may have been diminished by the high hydrologic loading rate into the mesocosm wetlands. *Typha* productivity was much higher than *Schoenoplectus* and was comparable to other field studies. *Schoenoplectus* wetlands responded with productivity that was low-to-average compared to natural wetlands but comparable to other mesocosm studies. The early senescence by Schoenoplectus in 2003 was likely an artifact of mesocosms and would not be expected in most shallow marshes.

The results of this study suggest that for a full-sized wetlands pulsing experiment as now underway at the ORW, pulsing may only show a negligible effect on *Typha* and *Schoenoplectus* productivity, given the high hydrological loading rate. However, there is several scale issues that should be considered before the results of this study are extrapolated to the full-size ORW wetlands. First, the full-sized wetlands encompass a large elevation range and will provide a greater range of inundated conditions. Second, even in areas that remain inundated, the greater exposure to wind fetch and water movement should alleviate the highly reduced conditions that may have negatively affected the *Schoenoplectus* in this study. Finally, the mesocosms had vegetation and soils that had only existed for one or two growing seasons while the full-sized wetlands have established vegetation and soils that have become depleted of Fe and available P and therefore may be more tied to fluctuating water levels to release organic-bound nutrients. Nevertheless, this study has demonstrated that *Typha* was more resilient to prolonged hydroperiods and may be better equipped physiologically than *Schoenoplectus* to withstand periods of anoxic that may occur during steady-flow hydrological regimes.

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